SYNONYMIZATION OF THE GENERA COMANTHERA AND CARPTOTEPALA WITH SYNGONANTHUS (ERIOCAULACEAE)¹

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ABSTRACT

The systematic positions of the monotypic Guayanan genera Carptotepala Mold. and Comanthera Lyman B. Smith are reevaluated. Carptotepala jenmanii (Gleason) Mold. is here placed in Syngonanthus sect. Thysanocephalus near S. xeranthemoides, under the name S. jenmanii (Gleason) Giulietti & Hensold. Comanthera kegeliana (Koern.) Mold. is here returned to Syngonanthus sect. Eulepis, as S. kegelianus (Koern.) Ruhl. Synonymies are given for each species.

The Eriocaulaceae, as currently treated, comprise 13 genera and about 1,200 species (Kral, 1989). The family has a pantropical distribution but is much more diverse and species-rich in South America, where two disjunct centers of diversity occur. These are the Cadeia do Espinhaço in Bahia and Minas Gerais, Brazil, and the Guayana Highland, especially in Venezuela. Although the largest concentration of species is found in the Brazilian center, the largest number of genera (10) is reported from Guayana.

Generic delimitations in the Eriocaulaceae are the subject of some controversy. The bulk of the species are contained in the large genera Eriocaulon L., Paepalanthus Kunth, Syngonanthus Ruhl., and Leiothrix Ruhl.; the remaining nine genera together contain only about 35 species. Of the five genera described since Ruhland's classic treatment (1903) (Carptotepala Mold., Comanthera Lyman B. Smith, Moldenkeanthus Morat, Rondonanthus Herzog, and Wurdackia Mold.), none were described with more than two species, and all but Moldenkeanthus of the Madagascar are endemic to the Guayana Highland. (Moldenkeanthus has recently been placed by Stützel (1987) in Paepalanthus.)

The systematic positions of Comanthera and Carptotepala have never been adequately investigated in publication, although some workers have informally expressed doubts about their validity (Moldenke, 1968, citing Görts-van Rijn; Giulietti, 1984; Stützel, 1985, in a footnote). Like all genera in the family, they are distinguished on the basis of floral characters, which often prove difficult to interpret in the extremely small flowers. We shall demonstrate here that these monotypic genera are indeed very closely allied with certain sections of Syngonanthus and that they lack any specialized characters to adequately distinguish them as genera in their own right.

I. CARPTOTEPALA

Moldenke (1951) described the genus Carptotepala based on C. insolita from Venezuela. Later he transferred Paepalanthus jenmanii Gleason, a species of British Guiana, to Carptotepala (Moldenke, 1957), and in 1968 he recognized C. insolita as a synonym of C. jenmanii. He distinguished the genus by the following characteristics: (1) free sepals and petals in both pistillate and staminate flowers; (2) prolongation of the floral

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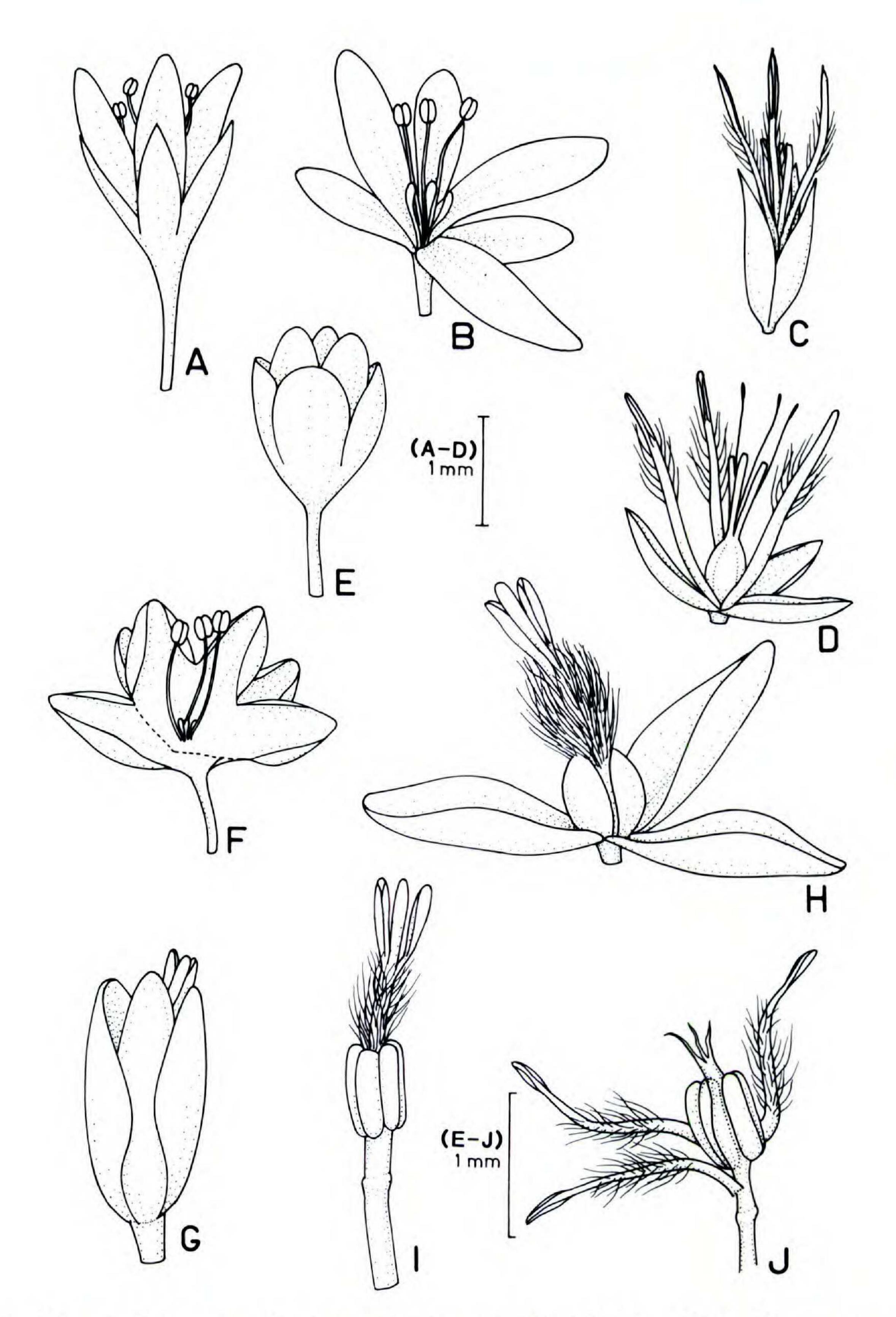


FIGURE 1. Flowers of Syngonanthus jenmanii (Gleason) Giulietti & Hensold and Syngonanthus kegelianus (Koern.) Ruhl. A-D. S. jenmanii (Jenman 7486 K). A, B. Staminate flower.—A. Whole flower.—B. Flower with perianth parts spread open to show stamens and pistillodes. C, D. Pistillate flower.—C. Whole flower at anthesis, the style tips barely protruding from the involute petal apices.—D. Flower with perianth parts spread open to show gynoecium. E-J. S. kegelianus (Lanjouw & Lindeman 2984 K). E, F. Staminate flower.—E. Whole flower.—F. Flower with perianth dissected open to show stamens and pistillodes. G-J. Pistillate flower.—G. Whole flower.—H. Flower with sepals spread apart, the petals remaining connivent around the style.—I. Flower after release of seeds, the sepals deciduous, the ovary locules open.—J. Same, with the petals dissected away.

receptacle above the calyx in the staminate flowers; and (3) presence of caudate appendages at the tip of the petals in the pistillate flowers.

In fact, the flowers of C. jenmanii are extremely similar to those of Syngonanthus, especially sects.

Thysanocephalus (Koern.) Ruhl. and Eulepis (Bong.) Ruhl., and may be compared as follows.

In Carptotepala jenmanii, the staminate flowers are found at the periphery of the capitulum and are much more abundant than the pistillate,

from which they are easily distinguished by their very long pedicels. These pedicels elevate the staminate flowers above the involucre, as is characteristic of sect. *Thysanocephalus*.

Also as in sect. Thysanocephalus, the sepals and petals of the staminate flowers are glabrous, concave, and similar to each other in size and texture (Fig. 1A, B). Contrary to the original descriptions of C. insolita and P. jenmanii, the sepals are united at the base, and the petals are briefly united or free. Moreover, we did not find elongation of the floral receptacle above the calyx (i.e., an "androphore"), as is known in some Syngonanthus (not sects. Eulepis or Thysanocephalus), and in most Paepalanthus and Eriocaulon. The description of an androphore in this species may have been due to misinterpretation of the fused basal portion of the corolla.

The pistillate flowers particularly recall sect. Thysanocephalus. In these the petals are densely pilose in the middle, and far surpass the sepals, with the glabrous apices curved around and enclosing the style branches. The tips of the style branches protrude slightly beyond the petals, and this apparently was misinterpreted by Moldenke as a "caudate appendage" (Fig. 1C, D).

The sepals and petals appear to be free, though the hairiness of the medial areas of the petals (where fusion normally occurs in *Syngonanthus*) makes it difficult to determine whether the petals are merely cohering about the style or truly fused.

Shallow or ephemeral corolla fusion in both staminate and pistillate flowers is recorded sporadically from sect. Thysanocephalus. Staminate flowers with petals nearly free are described for Syngonanthus squarrosus Ruhland (1903) and for S. chrysolepis Silveira (1928). Pistillate flowers with petals free or united medially are described for S. flexuosus Silveira, and petals connate but eventually separating are found in S. glaber Silveira (1928).

Moreover, complete loss of petal fusion in staminate and pistillate flower corollas, though rare, is found in Leiothrix fluitans (Mart.) Ruhl. and Rondonanthus (Paepalanthus) capillaceus (Klotzsch ex Koern.) Hensold & Giulietti (1991), two species whose closest relatives have the petals fused in at least the staminate flowers. These two species interestingly also share the rheophytic habit with C. jenmanii.

Thus, no reliable character remains for isolating this species from Syngonanthus sect. Thysanocephalus. The relationship is further supported by the characteristic campanulate to urceolate invo-

lucre found in Carptotepala and sect. Thysanocephalus. Inclusion of Carptotepala jenmanii within Syngonanthus is therefore proposed as follows.

Syngonanthus jenmanii (Gleason) Giulietti & Hensold, comb. nov. Paepalanthus jenmanii Gleason, Bull. Torrey Bot. Club 56: 14. 1929. Carptotepala jenmanii (Gleason) Mold., Mem. New York Bot. Gard. 9: 278. 1957. TYPE: Guyana. Potaro River, Kaieteur Savanna, Jenman 1032 (holotype, K).

Carptotepala insolita Mold., Fieldiana, Bot. 28: 114. 1951. TYPE: Venezuela. Bolívar: Rio Karuai, SW base of Ptari-tepui, 1,220 m, Steyermark 60703 (holotype, NY; isotype, F, GH).

Syngonanthus xeranthemoides var. grahamae Mold., Phytologia 8: 395. 1962. TYPE: Guyana. Potaro River, Mahdia goldfield, V. Graham 154 (holotype, K; isotype, LL). Syn. nov.

Additional specimens examined. VENEZUELA. BOLÍVAR: Canaima, Trujillo 6021 (MY, VEN); N Gran Sabana, Salto Aponwao, Huber & Entralgo 7399 (LL); Gran Sabana, Salto Camá, Davidse 4865 (MO); Ilú-tepui, Maguire 33516A (VEN). Guyana: Sandwith 1258 (K), Schomburgk s.n. (K); Upper Mazaruni River, Kamarang River, base of Utschi Falls, Tillett & Tillett 45744 (MO); Upper Mazaruni, Kako River, Tillett & Tillett 45486 (MO); Potaro River, Abraham 330 (K); Potaro River, Cobanatuk Falls, Jenman 7486 (K).

The closest affinities of Syngonanthus jenmanii appear to lie with the sympatric species S. xeranthemoides (C. Martius) Ruhl., which usually occurs on relatively drier sites. Syngonanthus jenmanii is distinguished within its section by its occurrence along wet riverbanks, in waterfall spray, and even occasionally with the leaves fully submerged.

II. COMANTHERA

Smith (1937) described the genus Comanthera to accommodate C. linderi Lyman B. Smith. He characterized the new genus by the presence of three distinct types of flowers: (1) the staminate, these pedicellate, with perianth reduced to a vestigial tubular sheath at the base of the flower, and with only one stamen, comose at the apex with long hairs; (2) the pistillate, these sessile, with sepals and petals free; and (3) the sterile, these also pedicellate, with the sepals and petals free.

Moldenke (1966) transferred the species Syngonanthus kegelianus (Koern.) Ruhl. to Comanthera, without discussion or further descriptive information. Two years later, he recognized C. linderi Lyman B. Smith as a synonym of C. kegeliana (Koern.) Mold. (1968). He also included in the

synonymy of this species S. akurimensis Mold. and S. akurimensis var. amazonicus Mold.

In the same article, he quoted a letter from A. Görts-van Rijn, who had studied type material of C. kegeliana, and questioned the validity of the genus. She compared the appearance of the staminate flowers in Smith's illustration (1937) "with the overripe female flowers, where the fruits have come out and the perianth segments had partly fallen off." Smith's reply in letter was also included, indicating that he was not convinced by her observations.

Because the perianth of eriocaulaceous flowers is chaffy and retains its form and color long after anthesis, differences between flowers at different stages may easily be misinterpreted as taxonomic differences. Therefore, flowers were examined from capitula of *C. kegeliana* in various stages of maturation. Only two types of flowers were observed, staminate and pistillate. At anthesis, these possess the following organization:

Staminate flower. Long-pedicellate; sepals three, free, glabrous; petals three, connate briefly at base, glabrous, somewhat surpassing the sepals; stamens three, the filaments filiform, included, anthers dithecous; pistillodes very small (Fig. 1E, F).

Pistillate flower. Short-pedicellate; sepals similar to those of staminate flowers; petals somewhat surpassing the sepals, connate and long-pilose medially, but separating very easily, free at apex and base, the apical portion somewhat broader than the medial portion and with the lateral margins involute, enclosing the styles; gynoecium with a three-locular ovary, and three elongate simple style branches slightly surpassing the petals (Fig. 1G, H).

The old flowers persist for some time in the head and present the following organization:

Staminate flower. Same as above, but the anthers lost and the filaments delicate and filiform.

Pistillate flower. After fertilization, the pedicels elongate considerably to equal those of the staminate flowers. A loculicidal capsule is formed with a membranaceous pericarp. After the liberation of the seed the two valves of each locule recurve toward the floral axis, completely enclosing the narrow bases of the petals. At the same time, the sepals fall, leaving only the pedicel and a small ring of tissue representing the scar where the sepals were inserted.

It is evident that the sterile, long-pedicellate flower portrayed in Smith's (1937) description and figures (pl. 2, fig. 59) is in reality a staminate flower that has lost its anthers after anthesis. The pistillate flower described and illustrated is in all respects like that of the material examined, except that the petals are depicted as free instead of connate medially. However, in dissection of pistillate flowers of this species it is quite easy to separate the pilose membranous petals without awareness of doing so. Smith described the flowers as sessile, but as noted, they are very short-pedicellate before fertilization, and may appear sessile in comparison to later stages of development. Moreover, truly sessile flowers are virtually unknown in Eriocaulaceae.

The staminate flower described and illustrated as possessing a single stamen comose at the apex is identical in appearance to the female flower after liberation of the seeds, as Görts-van Rijn suggested. The abscission scar left by the sepals corresponds to the reduced perianth described by Smith; the single dithecous anther corresponds to the two visible ovary locules with the pericarp completely recurved toward the center of the flower (the third locule is of course not evident as the flower is viewed from the side); and the comose apex of the "anther" corresponds to the narrow pilose segments of the petals, which project above the ovary, their bases hidden by the recurved locule walls.

The floral structure of Comanthera kegeliana and the variations found in progression from bud to fruiting are characteristic for the majority of species of the genus Syngonanthus, especially those of sect. Eulepis, in which S. kegelianus was first described.

It is therefore proposed that the genus Comanthera be synonymized with the genus Syngonanthus and its single species be placed in sect. Eulepis.

Syngonanthus kegelianus (Koern.) Ruhl., Pflanzenr. IV. 30: 273. 1903. Paepalanthus kegelianus Koern. in C. Martius, Fl. Bras. 33(1): 438. 1863. Dupatya kegeliana (Koern.) Kuntze, Revis. gen. pl. 2: 746. 1891. Comanthera kegeliana (Koern.) Mold., Phytologia 13: 218. 1966. TYPE: Surinam, Mariepaston, Kegel 1473 (holotype, GOET not seen, photo, K; isotype fragment, B not seen).

Comanthera linderi Lyman B. Smith, Contr. Gray Herb. 117: 38, pl. 2. 1937. TYPE: Guyana, Rockstone, Linder 40 (holotype, GH not seen; isotype, NY).

Syngonanthus akurimensis Mold., Phytologia 2: 371. 1947. TYPE: Venezuela. Bolívar: Cerro Akurimá, Tamayo 3234 (holotype, US not seen; isotype, NY). Syn. nov.

Additional material examined. VENEZUELA. BOLÍ-VAR: Lockhart s.n. (K); along Río Uairén, Lasser 1705 (F, VEN). GUYANA. Georgetown, Atkinson Field, Maas & Westra 3571 (K), McKee 10681 (K), Robertson & Austin 268 (NY); Rockstone, Gleason 652 (NY). SURI-NAM. Jodensavanne, Lanjouw & Lindeman 2984 (K).

Syngonanthus kegelianus is readily identified even from descriptions and photos because of the distinct pubescence on the leaves and peduncle sheaths of this species, i.e., stiff, erect hairs on leaf undersurface and appressed white malpighian scales on upper leaf surface and on peduncle sheaths. It is the only member of Syngonanthus sect. Eulepis found in the Guayana Highlands, and is fairly unusual within its section due to the small, hyaline, relatively unspecialized upper involucral bracts.

It has very close affinities with *Syngonanthus* ulei Ruhl. of Amazonian Brazil, which is only readily distinguished by the long spreading hairs on leaves and sheaths and the lack of white scalelike malpighian hairs. It may represent only a variety of *S. kegelianus*.

Syngonanthus akurimensis var. amazonicus Mold. (Phytologia 3: 42. 1948), which Moldenke considered synonymous with S. kegelianus, is probably identical with S. ulei, as is S. kuhlmannii f. viviparus Mold. (Phytologia 37: 97. 1977).

These new additions to the generic synonymy of Syngonanthus are summarized as follows:

Syngonanthus Ruhl. in Urban, Symb. Antill. 1: 487. 1900. TYPE: Syngonanthus umbellatus (Lam.) Ruhl. (Eriocaulon umbellatum Lam.).

Carptotepala Mold., Fieldiana, Bot. 28: 114. 1951. TYPE: Carptotepala insolita Mold.

Comanthera Lyman B. Smith, Contr. Gray Herb. 117: 38. 1937. TYPE: Comanthera linderi Lyman B. Smith.

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